

Positional Behavior of the White Uakari (*Cacajao calvus calvus*)

SUZANNE E. WALKER AND JOSÉ MÁRCIO AYRES

Department of Anthropology, Humboldt State University, Arcata,
California 95521 (S.E.W.) and Wildlife Conservation Society, Bronx,
New York 10460-1099 (J.M.A.)

KEY WORDS Pitheciini, Locomotor behavior, Postural behavior,
Brazilian Amazonia

ABSTRACT The positional behavior and habitat use of a group of white uakaries (*Cacajao calvus calvus*) was observed for 6 weeks in the dry season at Lake Teiú, Brazil. Data are presented for feeding, traveling, and resting activities. The most common feeding posture is sit, followed by stand. *Cacajao* frequently exhibits locomotor behaviors while in feeding trees, using pronograde clamber and quadrupedal walk. The most frequently used locomotor behaviors in travel are quadrupedal walk, leap, and pronograde clamber. Quadrupedal run and drop also figure importantly in the behavioral repertoire. The most frequent resting posture was sit, followed by ventral lie. Compared to representative members of the other pitheciin genera, *Pithecia* and *Chiropotes*, *Cacajao* engages in more locomotion while feeding, and uses more pedal suspension. While traveling, pronograde clamber and drop are more frequently used by *Cacajao*. Multiple, deformable supports are used more by *Cacajao* than by the other pitheciins throughout all activities. Overall, the positional behavior of *Cacajao* is more similar to that of *Chiropotes* than of *Pithecia*. *Cacajao*'s behavioral solutions to the problems of balance imposed by its greatly reduced tail are discussed. © 1996 Wiley-Liss, Inc.

Until recently, the pitheciins were virtually unknown in terms of any aspect of their natural behavior or ecology. In particular, few studies of *Cacajao* have been conducted; the only long-term field study to date is that of Ayres (e.g., 1986, 1989) on *Cacajao calvus calvus* at Lake Teiú in Brazil. *Cacajao calvus* is limited to the seasonally flooded *várzea*, forests of white-water rivers in western Amazonia (Ayres, 1989; Mittermeier and Coimbra-Filho, 1977).

A short-term study of the positional behavior of *Cacajao calvus calvus* was conducted from July to September of 1988 at Lake Teiú. The results of this study contribute to the growing body of knowledge on pitheciin behavior and ecology, as well as to that on platyrrhine positional behavior. Furthermore, comparisons are drawn between the positional behavior of *Cacajao* and that of the other pitheciin genera.

BACKGROUND

Cacajao is a member of the tribe Pitheciini, a group of specialized seed predators that also include the genera *Pithecia* and *Chiropotes* (e.g., Hill, 1960; Rosenberger, 1981; Ford, 1986; Kinzey, 1992). The pitheciins share a number of derived craniodental (Rosenberger, 1979) and postcranial (Ford, 1986) traits. *Cacajao* and *Chiropotes* share a number of derived features not shared with *Pithecia* (Rosenberger, 1988; Kay, 1990; Kinzey, 1992).

Two species of the genus *Cacajao* are recognized: *C. calvus* and *C. melanocephalus* (e.g., Hershkovitz, 1972; Mittermeier and

Received October 18, 1994; accepted April 22, 1996.

Address reprint requests to S.E. Walker, Department of Anthropology, Humboldt State University, 1 Harpst Street, Arcata, CA 95521.

Coimbra-Filho, 1977; Hershkovitz, 1987). *Cacajao calvus* includes a white form and a red form, *C. c. calvus* and *C. c. rubicundus*, respectively (e.g., Hershkovitz, 1972; Mittermeier and Coimbra-Filho, 1977). No published information exists on the behavior or ecology of *C. melanocephalus*; however, a long-term field study is currently in progress. (J. Boubli, personal communication).

Cacajao calvus calvus is found in the western Amazon basin, on the south bank of the Rio Solimões, with the Rio Japurá forming its eastern limit (Fontaine, 1981; Hershkovitz, 1987; Ayres, 1989). At Lake Teiú, Ayres (1989) estimated that *C. c. calvus* has a total home range size of 500–550 ha, but that use is concentrated on 250–300 ha.

Cacajao calvus is the largest of the pitheciin species; body weights average 3.8 kg for males and 3.1 kg for females (from Ford and Davis, 1992). This species exhibits little to moderate sexual dimorphism (Hill, 1960; Robinson et al., 1987), with females weighing approximately 81% of male body weight (based on Ford and Davis, 1992). *Chiropotes* is somewhat smaller than *Cacajao*. *Pithecia* is the smallest genus, with its members varying in body weight. The smallest species is *Pithecia pithecia*, which averages 1.8 kg for males and 1.4 kg for females (Ford and Davis, 1992). While *Chiropotes* and *Pithecia* have normal-length tails, *Cacajao* is the only neotropical primate with a greatly reduced tail, consisting of 17–18 vertebrae (Hill, 1960).

Fontaine (1981) documented the positional behavior of captive *Cacajao* living in a large, natural-type enclosure at Monkey Jungle, Florida. *Cacajao*'s primary locomotor mode was quadrupedalism, usually exhibited on solid boughs. Leaping was the second-most important behavior. Galloping and bounding were used for rapid locomotion, and crossed extension quadrupedal gaits for slow locomotion. For ascent of large boughs, *Cacajao* "often move by pushing in unison with the hindlimbs while using their forelimbs as pivot struts" (Fontaine, 1981:489). *Cacajao* crossed gaps by leaping, arm-swinging, or bridging. Individuals sometimes vertically clung, usually as a momentary pause between leaps. Some bipedal locomotion was observed in play or while food carrying, and

both bipedal suspension and bipedal standing were used in feeding. Long-term resting postures of *Cacajao* included the sprawl and a flexed resting posture, while the primary short-term posture was sitting. Fontaine noted differences in locomotion among age-sex classes. Adult males were slower and more cautious, and engaged in less leaping and arm-swinging than did females or juveniles. Bridging was more common in adults than in juveniles.

While the positional behavior of wild *Cacajao* had not been the focus of any study previous to the one reported on here, some locomotor data were collected from investigators focusing on other aspects of ecology (i.e., Ayres, 1986). Ayres collected preliminary data of locomotor behavior during bouts of travel for *C. c. calvus*. He found that quadrupedalism and leaping were the most important locomotor behaviors, with pronograde clambering ("climbing") frequently used as well.

STUDY SITE, STUDY GROUP

The study site was established as a biological reserve in 1987. It is located on the shores of Lake Teiú, a small oxbow lake between the Japurá River and Lake Mamirauá of northwestern Amazonas (3.22°S, 64.42°W), 47.5 km west of the town of Tefé (Ayres, 1986; Fig. 1). The mean temperature near the site (approximately 21 km to the southeast) was 29.5°C for 1984, and annual rainfall (between December 1983 and November 1984) was 2,850 mm (Ayres, 1986).

Cacajao occurs in a specialized habitat where much of the vegetation is seasonally inundated (Ayres, 1986, 1989; Johns and Ayres, 1987). The general habitat type covering the entire study area is *várzea*, which consists of the higher and lower *restingas* (levees) and *chavascal* (backswamp) (Ayres, 1986).

Mammalian diversity at Lake Teiú is low compared with that of terra firme areas (Ayres, 1986). *Cacajao* is sympatric at Lake Teiú with three other primate species, *Cebus apella*, *Alouatta seniculus*, and *Saimiri vanzolinii* (Ayres, 1986; Johns and Ayres, 1987), none of which has been the focus of study at this site. The low diversity of primate species

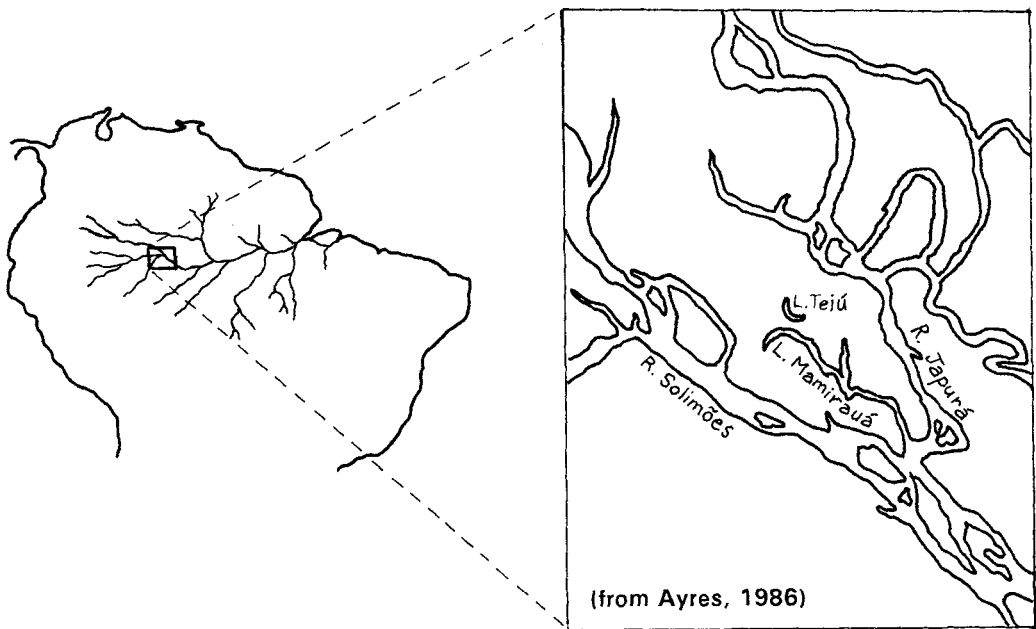


Fig. 1. Location of study site (Lake Teiú) in eastern Amazonas.

has been explained in terms of poor resource abundance and diversity (Ayres, 1986).

The trail system, developed by Ayres, includes more than 30 km of trails. The main study group of *Cacajao* consisted of 48–50 individuals, including multiple adult males and females and their offspring. As the dry season progressed and the water level dropped over the course of the study, fruit became increasingly sparse. The *Cacajao* group responded to the lower fruit availability by splitting into small feeding subgroups, which proved difficult to locate and follow. This seasonal variation in feeding group size is discussed by Ayres (1986).

METHODS

Observations were made at Lake Teiú for 6 weeks in 1988, from late July to early September. Data on a number of environmental and behavioral variables were collected using a focal animal instantaneous sampling technique (Altmann, 1977) at 2 min intervals. Due to the difficulty in finding and subsequently following *Cacajao*, an average of fewer than 3 hr of data per day was collected,

although total sampling covered most time periods of the day. Between 200 and 300 observations were recorded for each of the major activities (Feed, Travel, and Rest). Few individuals were identified due to the short-term nature of the study, the difficulty of following the animals, and their large group size.

An individual was selected at random, and observed for 5 sec before data collection began. It was observed until lost from view, at which time another (if possible from the same age–sex class and engaged in the same general activity) was selected and used as the focal animal. If no individual was in sight at the interval, data were recorded 5 sec after the next sighting to prevent biases in recording the most conspicuous behaviors.

The study of positional behavior presents problems in data analysis, due to the possible lack of independence of the sequential observations (e.g., Mendel, 1976; Cant, 1988; Dagosto, 1994), particularly for postural behaviors. Randomization techniques (as in Dagosto, 1994) could not be applied to these data, as the individuals of *Cacajao* were not

TABLE 1. Data on the following variables were collected using instantaneous focal animal samples

Time: Data were recorded at 2 min intervals.
ID of focal animal: Age/sex class.
Activity bout:
Travel: continuous movement, particularly between feeding trees or in long-distance travel; may include momentary pauses (<15 sec) while traveling.
Feed: preparation and ingestion of food. Also includes movement within a feeding tree, or carrying food.
Rest: nonmovement for at least 15 sec. Brief movements within an overall period of rest were scored as rest rather than travel if the individual moved for fewer than 5 sec.
Positional behavior: Postural or locomotor positions of the focal animal. For a detailed description of categories, see Walker (in press). The definitions of most of the positional behaviors do not vary between investigators; those that are used differently by various workers, or those which are relatively new, are defined below.
Postural behaviors: sit; stand; bipedal stand; perch: similar to sit, but the haunches are not involved in either weight bearing or balance—the weight is transmitted and the body balanced over the feet alone, which grasp the support, and tail may be draped over a branch for additional support; vertical cling; dorsal lie; ventral lie; lie on side; pedal suspension.
Locomotor behaviors: quadrupedal walk; quadrupedal run: distinguished from walk by opposite limbs striking support closer together in time, so gait usually approximates a trot, and speed of progression is increased; bounding/galloping is less frequently used, but the two are pooled here; pronograde clamber: movement across multiple substrates in a horizontal or diagonal direction (following Cant, 1988); pronograde clamber-run; climb: locomotion on supports with vertical or steeply sloping surfaces, with hindlimbs playing a greater propulsive role (following Rose, 1979; Cartmill, 1985); bridge; leap; drop: rapid descent with little or no propulsive exertion by the limbs, and little horizontal displacement.
Support number: One, two, or several (three or more) supports.
Support inclination: Horizontal (0–20°); angled (20–70°); vertical (70–90°); deformable (if support deformed under body weight); mixed (combination of supports of various angles).
Height—animal: Height from ground (in meters).
Location: Coordinates within trail system.

identified in this study. However, for purposes of statistical analyses (conducted elsewhere for these data: Walker, 1993b, in press), consecutive samples in which the positional behavior did not change can be pooled and counted as one sample (similar to Hunt, 1992). While not an ideal solution because of the loss of some data points, it does allow for the avoidance of nonindependent data (further discussed in Walker, 1993b, in press).

The following variables were recorded at 2 min intervals on a prepared data checksheet, and are defined in Table 1: time, age–sex class of focal animal, activity bout, positional behavior (including locomotor and postural behaviors), support number, support inclination (also for second support if leap involved), height of animal, and location.

The quantitative results are presented as frequencies of positional behavior and habitat use while engaged in the three major activities of Feed, Travel, and Rest. Since the goals of feeding, traveling, and resting are very dissimilar, one would expect that the means to achieve them would also differ. For example, previous studies (e.g., Fleagle and Mittermeier, 1980) have demonstrated that locomotor behavior differs greatly between Feed and Travel. Positional behaviors

involved in feeding are those that allow an individual to search for, harvest, and ingest food. Locomotion between feeding sites within a feeding tree constitutes part of the feeding strategy; therefore, those locomotor behaviors are analyzed with the other feeding positions. Likewise, postural behaviors, if exhibited as momentary pauses within a travel bout, are presented with travel behaviors. Resting activities may be punctuated by brief movement in the resting tree, primarily for repositioning or moving short distances to join other individuals.

These data on *Cacajao* are limited in that positional behavior during major activities other than Feed, Travel, and Rest was observed relatively infrequently, and not at all during sampling periods. Examples include play (observed numerous times) and copulation (observed once); quantitative data are presented for neither. Behaviors which did not represent at least 1.0% of the samples are pooled and represented by the category "other." In each of the positional behavior sections below, locomotor behaviors are reported first, followed by postural behaviors. The appendices present raw data for *Cacajao* together with comparative data for *Pithecia* and *Chiropotes*.

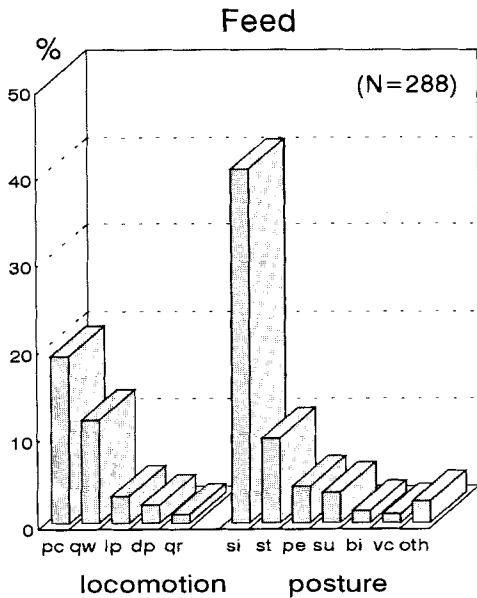


Fig. 2. Frequencies of positional behaviors used during feeding. Locomotor and postural behaviors: pc, pronograde clamber; qw, quadrupedal walk; lp, leap; dp, drop; qr, quadrupedal run; si, sit; st, stand; pe, perch; su, pedal suspension; bi, bipedal stand; vc, vertical cling; oth, other.

RESULTS

Positional behavior

Feed. Most positional behaviors used during feeding are postural; however, pronograde clambering and quadrupedal walk are also exhibited (Fig. 2). Other locomotor behaviors such as leap, drop, and run are rarely used during feeding. Overall, the primary posture used by feeding *Cacajao* is sit. Stand is used about one-fourth as frequently. Other postural behaviors—perch, pedal suspension, bipedal stand, and vertical cling—are seldom used during feeding.

Travel. The three primary behaviors used during travel are quadrupedal walk, leap, and pronograde clamber (Fig. 3). Quadrupedal run and drop were each observed about one-half as frequently as these primary behaviors. Pronograde clamber-run, climb up, and bridge are each used in few samples. The postural behaviors utilized in the mo-

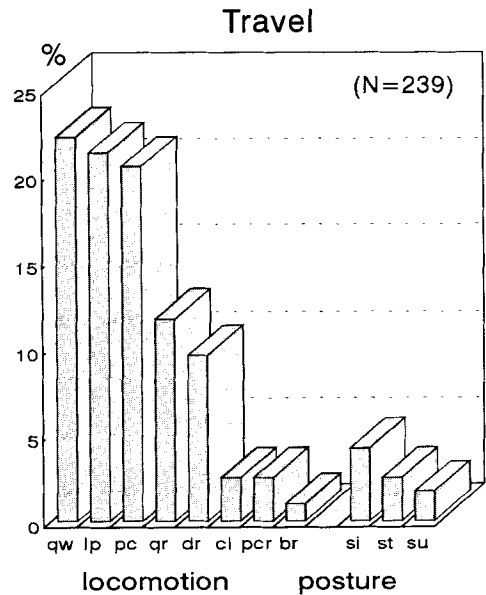


Fig. 3. Frequencies of positional behaviors used during travel. Abbreviations are the same as for Figure 2, with the addition of: cl, climb; pcr, pronograde clamber-run; br, bridge.

mentary pauses exhibited during travel are sit, stand, and pedal suspension.

Rest. While resting, *Cacajao* exhibits some brief movement using quadrupedal walk (Fig. 4). *Cacajao* uses sitting postures in almost two-thirds of rest bouts, and ventral lie in over one-fourth. Less frequently used behaviors include stand, lie dorsally and on side, vertical cling, and pedal suspension.

Height in tree, canopy level

The mean height at which *Cacajao* is found in the trees was 16.2 m. The height of the trees used is unknown; however, *Cacajao* most frequently uses the taller trees in the Teiú forest, which are between 20 and 35 m, for feeding (Ayres, 1986), and often for traveling. *Cacajao* most often used the upper or midupper portions of the forest (Ayres, 1986).

Support use

Feed. *Cacajao* uses several supports while feeding slightly more often than it uses a

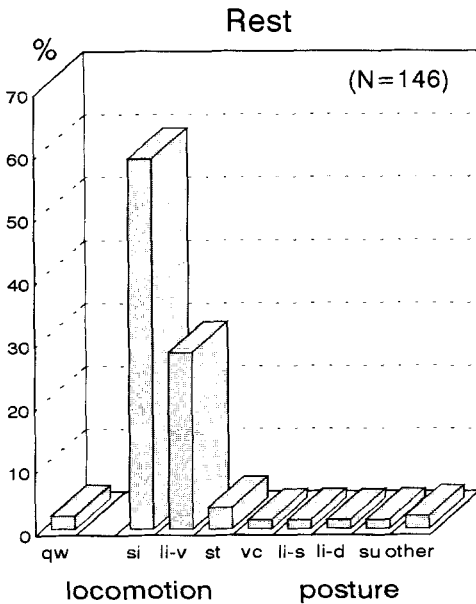


Fig. 4. Frequencies of positional behaviors used during rest. Abbreviations are the same as for Figure 2, with the addition of postural behaviors: li-v, lie on ventrum; vc, vertical cling; li-s, lie on side; li-d, lie on dorsum.

single support (Fig. 5). Two supports are used in only about 1/10 samples. The inclination of supports used in feeding is often indistinguishable because *Cacajao* frequently uses branches that deform under its body weight. These deformable supports are followed in frequency of use by horizontal supports (nondeformable). Angled supports are used less than half as often as either deformable or horizontal, followed by a mix of various support inclinations. Vertical supports are seldom used.

Travel. While traveling, *Cacajao* most frequently uses single supports (Fig. 5). Several supports are also often used, while the use of two supports in travel is rare. Again, supports that deform under body weight are more frequently used than those of known inclination, followed closely by horizontal then angled branches. A mix of various support inclinations, and vertical supports, are infrequently used.

Rest. *Cacajao* used a single support for the vast majority (almost two-thirds) of resting samples; in one-fourth of samples, use of two supports was recorded (Fig. 5). Several supports are used much less often for rest. *Cacajao* uses horizontal supports for resting over twice as often as it uses angled supports. Deformable branches are used in almost 1/10 of samples; neither vertical branches nor those of mixed inclination are common resting supports.

DISCUSSION

The positional behaviors exhibited by *Cacajao* during all major activities are apparently influenced by habitat structure in terms of canopy use and tree form, and by habitat use. Here, the positional behavior of *Cacajao* is compared to that of *Pithecia* and *Chiropotes*, for which data are presented in Appendices A and B.

Effects of habitat structure and habitat use on positional behavior

Feed. *Cacajao*'s positional behavior while feeding is determined by the characteristics and availability of supports in the tree portions where food is located. Primate food is often found in the terminal branches, or on small, flexible supports within the crown (e.g., Napier, 1967; Rose, 1974); therefore, *Cacajao* must employ specific strategies in order to reach it. Hindlimb suspension and bipedal stand are used to this end. Ayres (1986) mentions the use of hindlimb suspension for obtaining access to fruit, but points out that this behavior is used more often in play. *Cacajao* and *Chiropotes* both exhibit anatomical adaptations in the tarsal bones that are correlated with pedal suspension (Fleagle and Meldrum, 1988). However, *Cacajao* employs pedal suspension more frequently, and in a wider variety of contexts, than does *Chiropotes*.

Compared to the other pitheciins, and especially to *Pithecia* (Walker, in press), *Cacajao* exhibits more locomotor behavior during feeding (more movement within feeding trees). The primary locomotor behavior used while feeding is pronograde clamber, which is the consistently used mode for movement in terminal branches. Three factors may con-

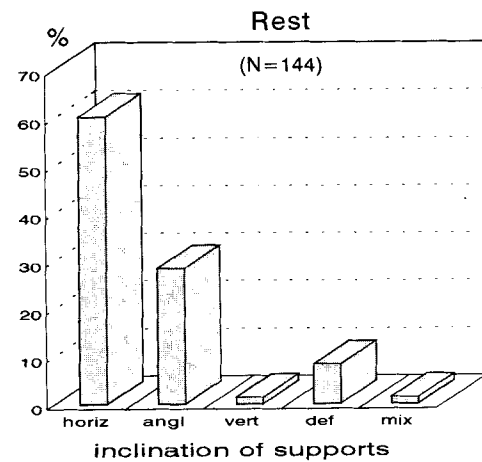
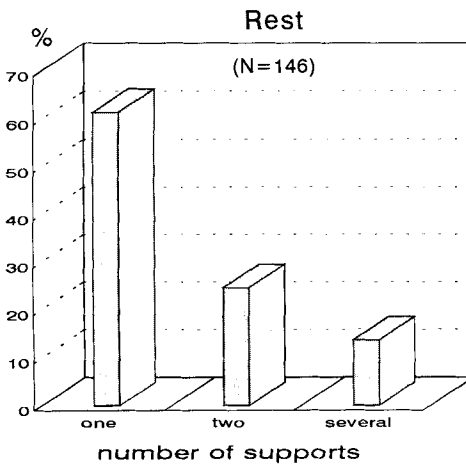
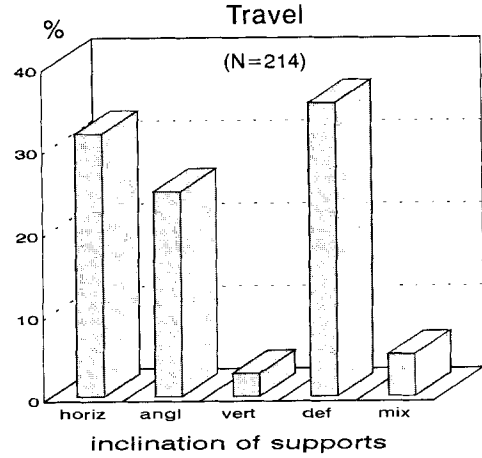
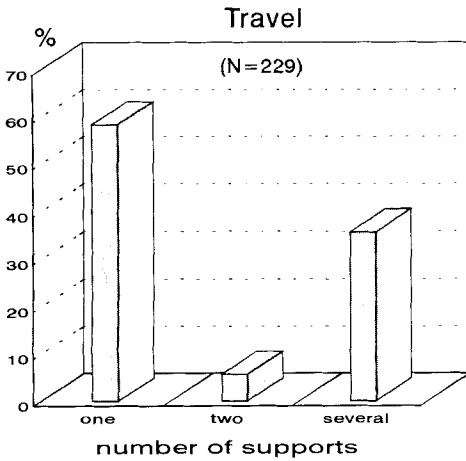
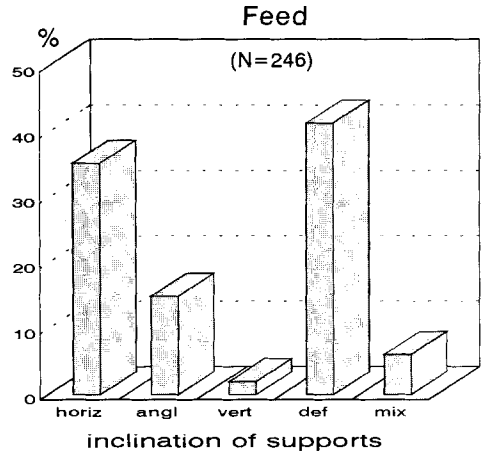
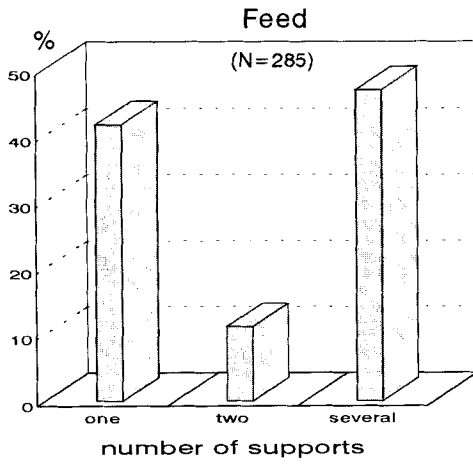


Fig. 5. Frequencies of support use. Top: feeding. Middle: travel. Bottom: rest. Left, number of supports: one, two, several. Right, inclination of supports: horiz, horizontal; angl, angled; vert, vertical; def, deformable (under body weight); mix, mixed.

APPENDIX A. *Frequencies of locomotor and postural behaviors (from Walker, in press)*

Positional behaviors N	Feed			Travel			Rest			Play Chir 175
	<i>Pith</i> 3,212	<i>Chir</i> 2,788	<i>Cacaj</i> 288	<i>Pith</i> 2,944	<i>Chir</i> 1,818	<i>Cacaj</i> 239	<i>Pith</i> 2,603	<i>Chir</i> 1,512	<i>Cacaj</i> 146	
Pron clmbr	10.4%	11.5%	19.1%	15.6%	16.7%	20.5%	0	0	0	4.6
Quad walk	1.5	5.3	11.8	15.1	22.9	22.2	0	1	2.1	0
Quad run	0	1.5	1.0	4.6	12.3	11.7	0	0	0	10.3
Leap	1.0	1.2	3.1	39.7	24.5	21.3	0	0	0	14.3
Drop	0	0	2.1	1.1	7.6	9.6	0	0	0	2.9
Climb	0	0	0	2.1	2.1	2.5	0	0	0	0
Hop	0	0	0	1.8	1.1	0	0	0	0	2.9
Pron cl-run	0	0	0	1.0	2.6	2.5	0	0	0	17.7
Bridge	0	0	0	0	2.0	1.0	0	0	0	0
Sit	53.3	51.0	40.6	6.4	2.9	4.2	72.9	56.8	58.9	16.7
Stand	9.8	12.8	9.7	2.1	3.3	2.5	2.5	5.0	3.4	6.3
Yert cl	10.5	0	1.0	3.6	0	0	11.3	0	1.4	1.1
Perch	9.3	8.3	4.2	0	0	0	0	0	0	1.1
Bip stand	1.7	3.5	1.4	0	0	0	0	0	0	2.3
Hind susp	0	1.2	3.5	0	0	1.7	0	0	1.4	17.1
Lie-ventrum	0	0	0	0	0	0	7.5	29.8	28.1	0
Lie-side	0	0	0	0	0	0	3.6	6.1	1.4	0
Lie-dorsum	0	0	0	0	0	0	0	0	1.4	1.1
Other	2.5	3.8	2.3	2.9	1.9	0.4	2.7	2.0	2.0	1.7

APPENDIX B. *Frequencies of support use (from Walker, in press)*

Support N	Feed			Travel			Rest			Play Chir 169
	<i>Pith</i> 3,167	<i>Chir</i> 2,778	<i>Cacaj</i> 285	<i>Pith</i> 2,779	<i>Chir</i> 1,762	<i>Cacaj</i> 229	<i>Pith</i> 2,606	<i>Chir</i> 1,513	<i>Cacaj</i> 146	
One	46.4	47.0	41.8	71.8	60.8	58.5	60.3	63.7	61.6	59.8
Two	15.4	20.2	11.2	7.1	8.1	5.7	31.9	29.8	24.7	8.9
Several	38.2	32.8	47.0	21.2	31.1	35.8	7.8	6.5	13.7	31.4
N	3,164	2,775	246	2,773	1,757	214	2,601	1,506	144	172
Horizont	16.8	24.8	35.4	20.5	24.9	31.8	34.1	56.0	60.4	27.9
Angled	26.0	23.8	15.0	35.2	33.8	24.8	40.7	32.9	28.5	24.4
Vertical	8.6	0	2.0	19.8	1.7	2.8	7.6	0	1.4	1.2
Deform	34.1	38.1	41.5	16.1	31.3	35.5	1.4	2.4	8.3	39.0
Mixed	14.5	12.9	6.1	8.4	8.4	5.1	16.2	8.5	1.4	7.6
N	3,158	2,777	No data	2,764	1,752	No data	2,602	1,506	No data	167
<2 cm	22.8	16.3	—	9.5	15.8	—	1.0	0	—	8.4
2-5 cm	37.5	37.6	—	42.7	28.7	—	44.8	20.7	—	30.5
6-10 cm	12.0	17.1	—	29.7	27.8	—	30.9	33.0	—	22.8
11-15 cm	3.0	3.9	—	6.1	9.9	—	5.8	18.8	—	9.6
>15 cm	1.0	1.6	—	1.3	3.4	—	0	12.2	—	4.8
Mix	24.0	23.6	—	10.7	14.4	—	17.6	15.3	—	24.0

tribute to the higher frequency of locomotion exhibited by feeding *Cacajao* compared to that observed for the other pitheciins. The first two factors apply as well to *Chiropotes*, which nevertheless engages less frequently in locomotor behaviors while feeding than does *Cacajao*. First, as described by Ayres (1986), *Cacajao* tends to move about in terminal branches to collect fruit, then carries it in the mouth to a more solid support. If little manipulation is required to open the fruit, *Cacajao* may eat it while traveling. For

eating hard fruits (frequently utilized by pitheciins), a hand may be needed to assist in stabilizing the food item in the mouth for puncture with the canines, eliminating the use of one forelimb for balance. This could result in the greater frequency of locomotion in feeding trees in order to seek out a solid support, or to encourage the spreading of weight over several supports. Both of these are exhibited more by *Cacajao* than by the other pitheciins. Second, the trees used by *Cacajao* tend to have large crowns, and therefore re-

quire more traveling within. The third reason is discussed in greater detail below, and relates to *Cacajao's* short tail and the resulting problems in maintaining balance.

Ayres (1989) found that *Cacajao* made extensive use of the ground, particularly in the driest months at Teiú. Over a particular period of 2 days in August of 1983, individuals were estimated to spend as much as 30–40% of their time foraging on the ground for seedlings of a species of Sapotaceae. Use of the ground during activities other than feeding was not observed. While *Pithecia* in Venezuela was observed coming to the ground occasionally to feed, these bouts totaled only about 1% of their feeding time, and *Chiropotes* was never observed feeding on the ground (Walker, 1993b). At Lake Teiú, two of the other three primates (*Cebus* and *Saimiri*) also use the lower forest levels when water level is low.

Ground use in *Cacajao* is probably made possible by the absence in the várzea habitat of many potential competitors, and by the rarity of terrestrial predators (Ayres, 1986, 1989). Throughout terra firme of Amazonia, the common competitors with *Cacajao* for fallen fruits are peccaries, paca, and agouti, which are notably absent from the site (Johns and Ayres, 1987). Even the avian fauna is distinct from that on terra firme, with a high diversity of aquatic species and relatively few terrestrial and understory species. Jaguar footprints were seen occasionally; these big cats travel over large home ranges, and are strong swimmers. This potential predator is presumed to have spent little time around the study site, since most of its common prey species (large terrestrial mammals) are absent. Also present, but relatively rare, are coatimundi and some of the smaller cats of the genus *Felis*. These latter carnivores probably rarely, if ever, prey upon *Cacajao*.

Terrestrial behavior was more frequently observed after a break in observations; upon detection of human observers, *Cacajao* returned to the trees. Therefore, the estimate of terrestriality in *Cacajao* may even be somewhat conservative. However, this information is based on a period of only 2 days; further observations throughout *Cacajao's* behavioral repertoire are necessary in order

to gauge the frequency and significance of its terrestrial behavior.

Travel. Like *Chiropotes*, *Cacajao* most often uses upper or midupper canopy levels, often moving through large trees that emerge above the surrounding vegetation. Since the various vegetation types diverge in height, individuals must often descend (or ascend) between trees. Often, *Cacajao* uses pronograde clambering to travel to the ends of the branches before bridging across to the terminal branches of a neighboring tree. *Cacajao* makes considerable use of these small, flexible supports for pronograde clambering as well as for the takeoff and landing supports used in leaping and dropping. These latter two locomotor modes are the most important gap-crossing behaviors for *Cacajao*. Although leaping plays an important role in *Cacajao's* locomotor repertoire, this taxon does not exhibit the anatomical specializations for leaping as seen in *Pithecia* (Fleagle and Meldrum, 1988). Also unlike *Pithecia*, which while leaping maintains a vertical body orientation and covers great horizontal distances, *Cacajao's* body orientation remains pronograde and its leaps often involve a downward component (Walker, 1993a). The leaping behavior of *Chiropotes* is similar to that of *Cacajao*.

For rapid travel, such as that used by *Cacajao* when the observer was detected, leaping was the primary locomotor mode used. Fontaine (1981) reported that captive *Cacajao* uses more leaping and armswinging when under stress. The use of frequent leaping was noted in unhabituated or startled individuals of the other two pitheciin genera as well (Walker, personal observation). In addition, leaping responses have been experimentally induced by playbacks of predators to colobus monkeys (Gebo et al., 1994). Thus, leaping may serve as a "critical" behavior in primate locomotion (Walker, 1993b). Most leaps and drops of *Cacajao* occur between the terminal branches of neighboring trees, and they are quite noisy. Neither *Cacajao* nor *Chiropotes* depend upon crypticity, while *Pithecia* clearly does. Vigilance, made effective by *Cacajao's* large group size, plays a more important role than any attempt at crypticity. For example, Ayres (1986) noted that only a few *Cacajao*

group members forage on the ground at a time, while others remain in the trees, presumably to keep watch.

Locomotion while suspended under supports by a combination of fore- and hindlimbs is very rare, but was observed for *Cacajao* in a few isolated incidents outside of the sampling period.

Rest. *Cacajao* does exhibit some brief locomotion during overall resting bouts, more so than the other pitheciins. This "repositioning" behavior may represent another effect of its reduced tail and the associated problems of maintaining balance.

While resting, *Cacajao* most often used single, horizontal supports; however, it also may use two or more. Sometimes these are located in or near the terminal branch portion of the tree. The use of these tree portions for resting may, as discussed by Ayres (1986), represent an anti-predator strategy, allowing good visibility as well as the probability of feeling any vibration in the tree which would indicate the presence of predators. *Cacajao*, like *Chiropotes* (Walker, 1993b), tends to use lower tree portions in the main crown during the day, and moves to higher, more distal tree portions at night. During day rest periods, only some group members sleep, while others play, groom, or simply rest without sleeping; the latter members can therefore remain vigilant. *Pithecia* remains on medium to large supports, often in dense vegetation, while sleeping.

During resting bouts, play was sometimes observed and noted (outside of sampling periods). Individuals often suspend themselves beneath flexible supports whose springiness is utilized to aid in play behaviors such as wrestling, or simply bouncing and swaying. Individuals may also swing while suspended by the hindlimbs; the flexed forelimbs are rapidly protracted and retracted to build momentum, swinging the entire body back and forth. This was observed several times in adults thought to be males, and is apparently used for display. This behavior was not observed in either of the other pitheciins.

Effect of reduced tail on *Cacajao's* positional behavior

Although *Cacajao* has a tail that is greatly reduced in length, both *Chiropotes* and

Pithecia have tails exceeding their body lengths. Tail use varies among primates (e.g., Rose, 1974), but plays important roles in communication, balance, or leaping behavior. *Cacajao*, like *Chiropotes*, exhibits vigorous tail wagging for communication and/or display. Tail wagging often occurs concurrently with vocalizations in both species, typically near the end of a rest period before troop movement begins. Tail twining, as discussed by Kinzey (1976) for *Callicebus*, is also exhibited by *Chiropotes* to a limited degree (Walker, 1993b), but not seen in *Pithecia*. *Cacajao's* tail is too short to engage in tail twining.

The best-documented use of nonprehensile tails is for balance (e.g., Cartmill and Milton, 1977). A tail that hangs straight down below a primate sitting on a branch can act to lower the animal's center of gravity toward the branch (Rose, 1974). The draping of a tail over a branch to assist in balance was also observed by Kinzey (1976), and noted for both *Chiropotes* and *Pithecia*, particularly while engaged in postural behavior in the terminal branches (Walker, 1993b). Tails may also guide direction or assist body rotation in leaps (Peters and Preuschoft, 1984; Dunbar, 1988).

Cacajao's tail is much too short to be used for balance or for guiding leaps. Comparisons with tail use in the other pitheciins may elucidate the implications of *Cacajao's* lack of a substantial tail for its positional behavior. Since the primary use of the tail in pitheciin positional behavior appears to be that of balance, particularly while engaged in postural behavior in terminal branches, *Cacajao* may solve its problems of balance by substituting other behaviors. While in terminal branches, *Cacajao* uses more hindlimb suspension and more locomotor behavior than do the other pitheciins, especially while feeding. Underbranch suspension has been discussed as a way to allow greater accessibility to food in the terminal branches (e.g., Grand, 1972). As a support becomes smaller (or body size larger), thereby narrowing the base of support, underbranch suspension may be made more feasible than balance on top of the support; anatomical features determine the efficiency of suspension compared to above-branch positions (e.g., Grand, 1972). Alternatively, a more solid support

can be used to suspend from in order to obtain food from terminal twigs that would themselves not support *Cacajao's* body weight. The greater problems faced by *Cacajao* in harvesting hard fruits, made more difficult without a long tail, have already been discussed. In addition, it is easier to move across small supports than to balance, unmoving, atop them. *Cacajao* also frequently extends the hindlimbs below the branch while sitting, which may serve to assist in balance by lowering the center of gravity.

Although the reason for *Cacajao's* tail having been reduced to a stump is unknown, it is assumed that selection pressures to have shortened the tail must have been quite strong to overcome the advantage of its use for balance. However, since a portion does remain, this indicates that those factors leading to tail reduction have not yet been strong enough to have completely overcome the selection pressure to maintain it for display. The smaller tail may have increased mobility, as the internal structure need not be as strong for a short tail as for a long one (Wilson, 1972).

Tail loss, or at least a reduction in number and/or size of caudal vertebrae, has also occurred in various groups of primates: the apes, some prosimians, and several species of primarily terrestrial cercopithecines. *Cacajao* is unique among platyrrhines in having a reduced tail. Models dealing with ambient temperature and body size, based on Allen's and Bergmann's rules, have been proposed for tail loss in the genus *Macaca* (Fooden, 1971); such models are untenable for *Cacajao*. Further observations may elucidate a selective advantage for *Cacajao's* short tail.

SUMMARY AND CONCLUSION

The positional repertoire of *Cacajao* consists primarily of quadrupedal behaviors such as quadrupedal walk and pronograde clamber, which are certainly expected for an arboreal primate of its body size. Leaping also plays a very important role; however, the qualitative characteristics of leaping are unspecialized when compared to *Cacajao's* close relative *Pithecia pithecia*, which exhibits behavioral and anatomical adaptations to leaping. The high degree of leaping in *Ca-*

cajao may be induced by the structure of its habitat, in which the vegetation varies greatly in height throughout the forest.

Behaviors which are particularly interesting in *Cacajao* are those involving bipedal suspension, and the high frequency of locomotion while in feeding trees. These are similar to *Chiropotes*, but more exaggerated in *Cacajao*, possibly relating to the reduced tail and the ensuing problems of balance, particularly in terminal branches. While the actual frequency of bipedal suspension in feeding *Cacajao* is relatively low (4%), it is thought to be significant due to the anatomical correlates for this behavior. In addition, future observations of longer duration may reveal a greater frequency of bipedal suspension. *Cacajao's* use of the ground may also be significant, particularly if the high frequency of ground use exhibited in only the 2 day period observed by Ayres (1989, 1986) is representative of its behavior over a longer term.

Relative to the other pitheciin genera, *Cacajao* may be more derived based upon its greater use of pedal suspension and its reduced tail, the latter of which is accompanied by behavioral differences in locomotion and posture. *Cacajao* has been forced to cope with the environmental pressures imposed by the drastic seasonal changes of its highly specialized habitat. In exhibiting terrestrial behavior, *Cacajao* demonstrates its dietary adjustment by utilizing an important portion of its habitat rarely used by other pitheciins in theirs.

ACKNOWLEDGMENTS

We are indebted to the Projecto Mami-rauá, and to Ibama for use of the floating house at the study site. Assistance in the field was provided by Chico dos Santos Martins. Funding for this study was provided by the Graduate Center of the City University of New York and by an Exploration Fund grant from the Explorer's Club (to S.E.W.). Dr. Elizabeth Strasser's helpful comments on the manuscript are much appreciated.

LITERATURE CITED

- Altmann J (1977) Observational study of behavior: Sampling methods. *Behaviour* 49:227-267.
- Ayres JM (1986) Uakaris and Amazonian Flooded Forest. Ph.D. Thesis, University of Cambridge.

- Ayres JM (1989) Comparative feeding ecology of the uakari and bearded saki, *Cacajao* and *Chiropotes*. *J. Hum. Evol.* 18:697-716.
- Cant JGH (1988) Positional behavior of long-tailed macaques (*Macaca fascicularis*) in Northern Sumatra. *Am. J. Phys. Anthropol.* 76:29-37.
- Cartmill M (1985) Climbing. In M Hildebrand, DM Bramble, KF Liem, and DB Wake (eds.): *Functional Vertebrate Morphology*. Boston: Harvard University Press, pp. 73-88.
- Cartmill M, and Milton K (1977) The loriform wrist joint and the evolution of "brachiating" adaptations in the Hominoidea. *Am. J. Phys. Anthropol.* 47:249-272.
- Dagosto M (1994) Testing positional behavior of Malagasy lemurs. A randomization approach. *Am. J. Phys. Anthropol.* 94:189-202.
- Dunbar DC (1988) Aerial maneuvers of leaping lemurs: The physics of whole-body rotations while airborne. *Am. J. Primatol.* 16:291-303.
- Fleagle JG, and Mittermeier RA (1980) Locomotor behavior, body size, and comparative ecology of seven Surinam monkeys. *Am. J. Phys. Anthropol.* 52:301-314.
- Fleagle JG, and Meldrum DJ (1988) Locomotor behavior and skeletal morphology of two sympatric pitheciine monkeys, *Chiropotes satanas* and *Pithecia pithecia*. *Am. J. Primatol.* 16:227-249.
- Fontaine R (1981) The uakari, genus *Cacajao*. In AF Coimbra-Filho and RA Mittermeier (eds.): *Ecology and Behavior of Neotropical Primates*. Rio de Janeiro: Academia Brasileira de Ciencias, pp. 443-494.
- Fooden J (1971) Female genitalia and taxonomic relationships of *Macaca assamensis*. *Primates* 12:63-75.
- Ford SM (1986) Systematics of the New World Monkeys. In DR Swindler and J Erwin (eds.): *Comparative Primate Biology, Vol. 1: Systematics, Evolution and Anatomy*. New York: Alan R. Liss, pp. 73-135.
- Ford SM, and Davis LC (1992) Systematics and body size: Implications for feeding adaptations in New World monkeys. *Am. J. Phys. Anthropol.* 88:415-468.
- Gebo DL, Chapman CA, Chapman LJ, and Lambert J (1994) Locomotor response to predator threat in red colobus monkeys. *Primates* 35:219-223.
- Grand TI (1972) A mechanical interpretation of terminal branch feeding. *J. Mammal.* 53:198-201.
- Hershkovitz P (1972) Notes on New World monkeys. *Intl. Zoo Yearb.* 12:3-12.
- Hershkovitz P (1987) Uacaries, New World Monkeys of the genus *Cacajao* (Cebidae, Platyrrhini): A preliminary taxonomic review with the description of a new subspecies. *Am. J. Primatol.* 12:1-53.
- Hill WCO (1960) *Primates: Comparative Anatomy and Taxonomy, Vol. IV*. Edinburgh: Edinburgh University Press.
- Hunt KD (1992) Positional behavior of *Pan troglodytes* in the Mahale mountains and Gombe Stream National Parks, Tanzania. *Am. J. Primatol.* 87:83-105.
- Johns AD, and Ayres JM (1987) Conservation of white uacaries in Amazonia várzea. *Oryx* 21:74-80.
- Kay RF (1990) The phyletic relationships of extant and fossil Pitheciinae (Platyrrhini, Anthroipoidea). In JG Fleagle and AL Rosenberger (eds.): *The Platyrrhine Fossil Record*. New York: Academic Press, pp. 175-208.
- Kinzey WG (1976) Positional behavior and ecology in *Callicebus torquatus*. *Yearb. Phys. Anthropol.* 20:468-480.
- Kinzey WG (1992) Dietary and dental adaptations in the Pitheciinae. *Am. J. Phys. Anthropol.* 88:499-514.
- Mendel F (1976) Postural and locomotor behavior of *Alouatta palliata* on various substrates. *Folia Primatol.* 26:36-53.
- Mittermeier RA, and Coimbra-Filho AF (1977) Primate conservation in Brazilian Amazonia. In Prince Rainier of Monaco and G Bourne (eds.): *Primate Conservation*. New York: Academic Press, pp. 117-167.
- Napier J (1967) Evolutionary aspects of primate locomotion. *Am. J. Phys. Anthropol.* 27:333-342.
- Peters A, and Preuschoft H (1984) External biomechanics of leaping in *Tarsius* and its morphological and kinematic consequences. In C Niemitz (ed.): *Biology of Tarsiers*. New York: Gustav Fischer Verlag, pp. 227-255.
- Robinson JG, Wright PC, and Kinzey WG (1987) Monogamous cebids and their relatives: Intergroup calls and spacing. In BB Smuts, DL Cheney, RM Seyfarth, RW Wrangham, and TT Struhsaker (eds.): *Primate Societies*. Chicago: Chicago University Press, pp. 44-53.
- Rose MD (1974) Postural adaptations in New and Old World monkeys. In FA Jenkins (ed.): *Primate Locomotion*. New York: Academic Press, pp. 201-222.
- Rose MD (1979) Positional behavior of natural populations: Some quantitative results of a field study of *Colobus guereza* and *Cercopithecus aethiops*. In ME Morbeck, D Preuschoft, and N Gomberg (eds.): *Environment, Behavior and Morphology: Dynamic Interactions in Primates*. New York: Gustav Fischer Verlag, pp. 75-94.
- Rosenberger AL (1979) Phylogeny, Evolution and Classification of New World Monkeys (Platyrrhini, Primates). PhD. Thesis, City University of New York.
- Rosenberger AL (1981) Systematics: The higher taxa. In AF Coimbra-Filho and RA Mittermeier (eds.): *Ecology and Behavior of Neotropical Primates*. Rio de Janeiro: Academia Brasileira de Ciencias, pp. 419-442.
- Rosenberger AL (1988) Pitheciinae. In I Tattersall, E Delson, and J van Couvering (eds.): *Encyclopedia of Human Evolution and Prehistory*. New York: Garland Publishing, pp. 454-455.
- Walker SE (1993a) Qualitative and quantitative differences in leaping behavior between *Pithecia pithecia* and *Chiropotes satanas*. *Am. J. Phys. Anthropol.* 16: 202-203.
- Walker SE (1993b) Positional Adaptations and Ecology of the Pitheciini. Ph.D. Thesis, City University of New York.
- Walker SE (in press) Evolution of positional behavior in the saki/uakaris (*Pithecia*, *Chiropotes*, *Cacajao*). In M Norconk, A Rosenberger, and P Garber (eds.): *Advances in Primatology: Adaptive Radiations of Neotropical Primates*. New York: Plenum.
- Walker DR (1972) Tail reduction in *Macaca*. In R Tuttle (ed.): *The Functional and Evolutionary Biology of Primates*. New York: Aldine-Atherton, pp. 241-261.